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EFFECTS OF UNILATERAL MESENCEPHALIC RETICULAR
FORMATION LESIONS ON MONOCULAR DISCRIMINATION PERFORMANCE
IN THE RAT

by



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A THESIS

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Abstract

The effects of mesencephalic unilateral formation

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Effects of Unilateral Mesencephalic Reticular Formation Lesions on Monocular Discrimination Performance in the Rat", submitted by Theodore Donald Weiden in partial fulfillment of the requirements for the degree of Master of Science.

Abstract

The effects of mesencephalic reticular formation (MRF) lesions ipsilateral and contralateral to the side of visual input were examined in unilaterally enucleated rats during the performance of a variety of brightness discrimination tasks in a parallel alley maze. It was found that small unilateral MRF lesions did not markedly interfere with the performance of a simple discrimination task learned prior to lesioning. However, Ss with lesions contralateral to the side of visual input showed a greater increase in choice- and run-speed during retention testing than those with ipsilateral lesions. On the other hand, when the luminance of the positive discriminandum was progressively lowered the contralateral group tended to make more errors than the ipsilateral group. Moreover, during reversal discrimination training the contralateral group started slower, chose, and ran slower on the initial trials of a training session, and ran slower during the earlier stages of training than the ipsilateral group. Taken together, these findings were interpreted to suggest that unilateral MRF lesions affect the performance of visually guided tasks in a unique and subtle manner when such tasks are mediated by the visual field contralateral to the side of the lesion. These data were discussed in terms of an hypothesis involving a deficit in visual orienting activity.

In addition, this study showed that MRF lesioned Ss tended to make more errors when reward was on the side opposite that of their lesion during the performance of a discrimination task learned prior to lesioning and during the early stages of reversal discrimination training than they did when reward was on the same side. This finding was interpreted as a preference for MRF lesioned Ss to turn to the same side as that of their lesion. These data tend to support the hypothesis that damage to fibers of the tectospinal tract at the level of the midbrain result in an ipsiversive turning preference.

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Introduction

In a recent study, Walley and Fedora (1969) noted that rats with stimulating electrodes placed unilaterally in the mesencephalic reticular formation (MRF) tended to make more errors when reward was on the side contralateral that of their electrode placement during the acquisition of a brightness discrimination task in a parallel alley maze. Since this tendency did not depend on whether or not the brain was stimulated, it was hypothesized that the small lesion produced by the stimulating electrode caused this behavior. In a subsequent study (Walley and Weiden, 1969), rats were lesioned unilaterally in the MRF and tested for retention of a similar brightness discrimination problem learned prior to lesioning. A tendency to make more errors when reward was on the side contralateral that of the lesion was again observed. Though this finding supports the hypothesis that unilateral lesions of the MRF cause a decrement in the performance of a visually guided task, the nature of the lesion produced deficit could not be ascertained. That is, it was not clear whether MRF lesions result in a motor bias for turning to the same side as that of the lesion or whether such lesions produce a perceptual deficit in the visual field contralateral to that of the lesion.

A recent wave of interest in the role of midbrain mechanisms subserving visually guided behavior in the mammal has been stimulated

by the work of Sprague and his colleagues (Sprague, Chambers and Steller, 1961; Sprague, Levitt, Robson, Liu, Steller and Chambers, 1963; Sprague and Meikle, 1965). In the final study of this series (Sprague and Meikle, 1965), two dissociable deficits in visually guided behavior were reported to arise from unilaterally placed midbrain lesions in the cat. These deficits were described as: (1) a neglect of visual stimuli in the contralateral visual field, and (2) a disruption of the motor component of the visual orienting response to the side contralateral to that of the lesion. The motor component of the visual orienting response is defined as those movements of the head, neck, and body which are involved in orienting to and in visually following the movement of a stimulus (i.e., a piece of fresh meat) across the visual field. A tendency for ipsiversive turning that was seen to occur after unilateral midbrain lesions was interpreted as a consequence of the lateralized disruption in the motor component of the visual orienting response. Visual neglect, or a deficit in visual "attention", is defined as the absence of any overt response to the stimulus, e.g., grasping, approaching, or orienting to it.

Sprague and Meikle (1965) suggest that the superior colliculus is the midbrain structure responsible for visual attention as well as bodily movements involved in visual orienting activity. Interruption of specific input and output pathways

resulted in the dissociation of these two components. That is, lesions involving the tectospinal tract were reported to cause the motor deficit, whereas lesions involving the brachium of the superior colliculus and the tectothalamic fibers reportedly caused the attentional deficit.

In a more recent study, Schneider (1969) reported no deficit in identifying patterns or discriminating black and white discriminanda after undercutting the superior colliculus in the hamster. However, when Ss were required to make visually guided orienting movements towards the stimuli, a severe deficit was observed. This deficit was described as an inability in localizing stimuli in the contralateral visual field. In addition to this deficit, Schneider (1969) reports a tendency for ipsiversive turning following such lesions. This behavior does not appear to be dependent upon visual input, however, for a preference for ipsiversive turning could be observed equally well in the dark.

In Schneider's (1969) study, the superior colliculus was seen to be the midbrain structure responsible for the integration of visually guided behavior involved in the localization of visual cues. Interruption of the brachium of the superior colliculus, the pathway for retinal and cortical input to the superior colliculus (Sprague and Meikle, 1965), resulted in the localization deficit, whereas interruption of descending tectal fibers resulted in ipsiversive turning in addition to the localization deficit.

Though the above studies have stressed the role of the superior colliculus in visually guided behavior, midbrain structures other than the superior colliculus have been implicated in the performance of visual discrimination habits in the rat (Thompson, 1969). Using the lesioning technique, Thompson (1969) has delineated a neurological system that appears to be critical for the retention of a wide variety of visual discrimination tasks. The midbrain component of this system is said to extend from the posterior thalamus to the ventromedial mesencephalon. Unfortunately, however, the experimental manipulations in this study do not allow one to determine whether perceptual or motor dysfunctions underlie the deficits in performance that arise following lesions in this system.

Behaviorally, the role of the MRF in visually guided behavior is uncertain. Fuster (1968) reported that electrical stimulation of the MRF in monkeys improved performance on a visual discrimination task. Walley and Fedora (1969), however, were not able to find any improvement in performance following unilateral stimulation of the MRF in rats during the acquisition of a brightness discrimination task in a parallel alley maze. Turning to lesioning studies, Kesner, Fiedler and Thomas (1967) found that bilateral lesions of the MRF did not markedly interfere with the learning ability of rats in visually guided tasks such as active avoidance or performance in the Lashly III maze. On the other hand, such preparations were seen to

exhibit less orienting activity than normals when a novel stimulus was presented during the performance of a learned task (Kesner and Vredenburg, 1970).

Notwithstanding the lack of consensus in behavioral studies, anatomical and physiological considerations suggest that the reticular core of the brainstem at the level of the mesencephalon may mediate some unique function with regard to visually guided behavior. Sokolov (1960), for instance, suggests that the MRF functions as a neurological amplifying system and that this system underlies the development of the orienting response. The concept of the MRF as a neurological amplifying system is consonant with a variety of anatomical and physiological data. The existence of fiber tracts that project both rostrally and caudally from brainstem reticular systems have been seen to modulate the degree of synaptic drive on neurons spread widely throughout the forebrain, brainstem, and spinal cord (Scheibel and Scheibel, 1967). In particular, electrical stimulation of the MRF has been noted to facilitate the reactivity of some neurons in the lateral geniculate body (Ogawa, 1963). Stimulation of this area has also been noted to facilitate spinal reflexes as well as cortically evoked movements (Magoun and Rhines, 1946; 1947).

Since there appears to be a fair degree of lateralization of motor output at the level of the midbrain (Schneider, 1969; Skultety, 1962; Sprague and Meikle, 1965) and since the visual system is almost

entirely crossed in the rat (up to 95% of the rat's retinal fibers cross the optic tract; Hayhow, Sefton and Webb, 1962), the combination of unilateral MRF lesions and unilateral enucleations may reveal deficits in visually guided behavior in the rat that are dissociable as either perceptual or motor in origin. More specifically, if unilaterally placed MRF lesions produce deficits in motor movements to the contralateral side, the performance of a visually guided task in a parallel alley maze should be impaired on those trials in which reward is on the side contralateral that of the lesion regardless of the side of visual input. On the other hand, if the MRF lesion produces a deficit in the perception of stimuli in the contralateral visual field, the performance of a monocularly mediated visually guided task should be impaired when the eye on the side contralateral to that of the lesion is being used.

In the first experiment of this study, retention of a monocularly mediated simultaneous brightness discrimination task is examined following unilateral MRF lesions.

Experiment 1

Method

Subjects. The Ss were 24 male albino rats of the Wistar strain purchased from Woodlyn Farms Limited, Guelph, Ontario. Each rat weighed between 250 and 325 gm. at the start of the experiment. Two Ss died while undergoing surgery and a third was sacrificed due to a post-operative eye infection.

Apparatus. The apparatus was a two choice parallel alley maze similar to that used by Walley and Fedora (1969). This maze consisted of a start box, a choice chamber, and two alleys, all painted gray. Just above the food cup at the end of each alley, a 25-Watt incandescent bulb was covered by a 4.5 in. x 9 in. panel of flashed opal glass. Midway down each alley an archway and an accompanying guillotine door, also painted gray, were inserted. The positive discriminandum became light emitted through the opened archway from the flashed opal glass panel at the end of the alley. Lowering one of the archway doors had the effect of sealing off the terminal half of that alley from motor and visual inspection. In addition, an inverted plexiglass guillotine door separated the start box from the choice chamber. The archway door was operated manually prior to a trial, whereas the start box door was operated remotely from a control booth directly behind the apparatus at the beginning of each trial.

Located in the same control booth were three Hunter model 120A Klockcounters. Lowering the start box door started the first timer. This timer was stopped and a second one started when S broke a light beam located 2 in. from the start box door. The second timer was stopped and a third started when S broke a light beam which passed through both alleys at a distance of 5 in. past the choice point. The third timer was stopped when S broke the final light beam which also passed through both alleys at a distance of 14.5 in. from the second one. The three timers yielded start-, choice-, and run-time measures, respectively.

Eight holding boxes were used to hold Ss during intertrial intervals. Each box consisted of four walls and a hinged lid, all of which were painted gray. Water was available in the holding boxes as well as in the home cages throughout the experiment.

Procedure. Five days after surgically removing the left eye of each S, a food-deprivation schedule was initiated which was adjusted to maintain body weight at approximately 85% normal growing weight. Two days after beginning the food-deprivation schedule, Ss were placed in the apparatus, 4 at a time, and allowed to explore for 15 min. a day. During this period, food pellets (Noyes Precision Food Pellets; 45 mg. each) were placed in the food cups at the end of each alley. This adaptation and exploration procedure was carried out for the following 4 days.

Training: Subjects were given 10 simultaneous brightness discrimination training trials per day until a criterion of 19 correct trials within two consecutive days was reached. A trial consisted of removing S from a holding box and placing him into the start box so that he faced the front of the apparatus. The inverted plexiglass start box door was lowered swiftly and steadily after S had turned around and moved up to it. Once in the choice chamber, the start box door was raised to prevent retracing. The opened archway door midway down the lighted or "correct" alley allowed S to reach the food cup at the end of that alley and receive a reward of 3 food pellets. The position of the correct alley was determined by a pre-arranged Gellerman sequence. The closed archway door midway down the non-lighted or "incorrect" alley prevented S from reaching the end of that alley. An error was recorded when S broke the choice time light beam in the incorrect alley (i.e., 5 in. past the choice point). A correction procedure was employed throughout the experiment. Following a trial, S was removed to a second holding box to wait out a 3-4 min. intertrial interval. All Ss were fed approximately 1 hr. after being returned to their home cages.

Upon reaching criterion, Ss were randomly assigned to either a right or a left MRF lesion group and lesioned accordingly on the following day.

Testing: After surgery, Ss were allowed to recover for 5 days on an ad lib food schedule. During this time, they were periodically checked for overt anomalies in visual and motor behavior with the following clinical tests: (1) turning preference when placed on a clear table top; (2) motor coordination in climbing between E's hands, and (3) symmetry in muscular tonus as revealed by suspending the rat in midair by it's tail.

Five days after surgery, Ss were placed back on the food-deprivation schedule. Three days after reinstating the food-deprivation schedule, testing began for retention of the discrimination problem. This test was carried out over the next 4 days under the same procedure used during training.

Surgery. All surgery was performed under deep pentobarbital anesthesia according to the method described by Rye and Elder (1966).

Enucleation consisted of grasping the left orbit with a pair of forceps and completely cutting all muscle and nerve attachments to it. The empty socket was then filled with sterile Gelfoam and sutured closed.

Brain lesions were produced by a Grass LM4 Lesion Generator, using an insulated stainless steel electrode with an exposed tip of 0.5 mm. A voltage of 25V. delivered for 30 sec. was used to create a lesion of somewhat less than 1 mm. in diameter.

Unilateral lesions of the MRF were placed with the aid of a Kopf stereotactic instrument, using the following coordinates: 1.7 mm. anterior, 1.8 mm. lateral, and 0.6 mm. below horizontal zero (König and Klippel, 1963).

Histology. After completion of all post-lesion experiments, Ss were sacrificed with an overdose of pentobarbital and perfused intracardially with normal saline followed by 10% formalin. The brains were then removed and placed into jars filled with 10% formalin for at least 48 hrs. before being sectioned on a freezing microtome at a thickness of 50 μ . Every third section showing the lesion was mounted on a glass slide and photographed against a dark background with illumination from the side.

Results

Histological. Inspection of the brains made it necessary to eliminate 5 Ss from the study. No lesion could be found in 4 of these Ss even though an electrode track was generally visible. A faulty ground connection noted during lesioning may account for the absence of a lesion in these Ss. In the fifth S, the lesion was found to be located in the medial geniculate nucleus.

One S (S #10) sustained damage to the superior colliculus in the vicinity of the descending electrode track, though at a considerable distance from the site of the MRF lesion. He was retained in the study, however, when no aberrant behavior could be detected in his

records. Of the 16 Ss retained in the study, 8 were found to have a lesion on the right side of the MRF, and 8 on the left (see Figure 1).

Pre-lesion training data. An analysis of variance involving experimental lesion groups and side of reward was performed on the mean number of errors made during the entire training period. No significant differences were found. In addition, a 4-way analysis of variance involving experimental lesion groups, days, side of reward, and trials was performed on error and speed data acquired on the last 2 days before reaching criterion. In this analysis, 4 dependent variables were analyzed: (1) transformed errors ($\sqrt{X+0.5}$), (2) start-speed, (3) choice-speed, and (4) run-speed. All time measures were reciprocally transformed to yield speed measures. This analysis revealed a significant decrease in the number of errors made over trials ($F = 3.364$, $df = 4/56$, $p < .05$) as well as a significant increase in run-speed over days ($F = 8.487$, $df = 1/14$, $p < .05$) and trials ($F = 2.547$, $df = 4/56$, $p < .05$). Means for these analyses can be found in Tables 1 and 2 of the Appendix, respectively.

The absence of any significant differences between experimental lesion groups in either of these analyses indicates that the experimental groups were similar in their pre-lesion performance. Moreover, symmetry of the apparatus is indicated by the absence of any significant differences in performance with regard to side of reward.

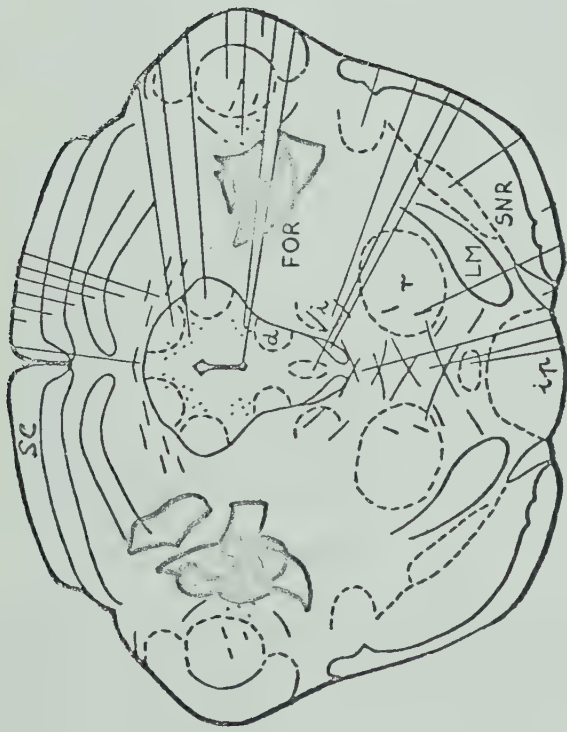


Figure 1

A composite reconstruction of MRF lesion damage at its largest extent ($A 1610_{\mu} \pm 500_{\mu}$; Konig and Klippel, 1963). Abbreviations: FOR = reticular formation, ip = interpeduncular nucleus, LM = medial lemniscus, r = red nucleus, SC = superior colliculus, SNR = substantia nigra.

Post-lesion retention data. In this experiment, differences between pre- and post-lesion performance scores were analyzed by the same 4-way analysis of variance design used for the pre-lesion criterion data. Individual difference scores were obtained by subtracting mean pre-lesion performance scores acquired on the last 2 days before reaching criterion from post-lesion scores achieved during the retention test. All data were transformed in the same manner as the pre-lesion criterion data.

This analysis revealed a significant decrease in the number of errors made over days ($F = 3.842$, $df = 3/42$, $p < .05$). Means for these effects can be seen in Table 3 of the Appendix. In addition, the error data revealed a significant interaction between lesion groups and side of reward ($F = 4.826$, $df = 1/14$, $p < .05$). As can be seen in Table 1, the means for this interaction indicate that Ss tended to make more errors when reward was on the side contralateral that of their MRF lesion. Caution should be used in interpreting this result, however, since very few errors were made during the retention test (only 35 errors in 640 trials).

Start-speed data did not reveal any significant effects. However, a significant increase in choice-speed was found over days ($F = 16.297$, $df = 3/42$, $p < .01$) and trials ($F = 21.142$, $df = 4/56$, $p < .01$). These means can be seen in Tables 3 and 4 of the Appendix, respectively. Choice-speed data also revealed a significant interaction between lesion groups and days ($F = 3.579$, $df = 3/42$, $p < .05$).

Table 1

Differences in Pre- and Post-lesion Mean Errors
(per day) between Experimental Groups and Side
of Reward During Retention Testing.

Lesion Group	Side of Reward	
	Right	Left
Right	-0.006	0.026
Left	0.023	0.000

Means for this interaction can be seen in Figure 2. In an effort to clarify this interaction, differences between means for right and left lesion groups on each of the 4 test days were subjected to Duncan's New Multiple Range Test (Edwards, 1960). This test revealed that the group mean difference for Day 1 was significantly different than that for Day 3 ($p < .01$) and Day 4 ($p < .01$). Moreover, the group mean difference for Day 2 was significantly different than that for Day 3 ($p < .05$). Essentially, this analysis shows that the left lesion group tended to choose more slowly than the right lesion group on the first day of retention testing, but that this difference was significantly reversed by the third day.

Similar effects were noted in the run-speed data in that Ss tended to run faster over days ($F = 14.284$, $df = 3/42$, $p < .01$) and trials ($F = 7.811$, $df = 4/56$, $p < .01$), and lesion groups were seen to interact significantly with days ($F = 4.227$, $df = 3/42$, $p < .05$). Means for the days and trials effects can be seen in Tables 3 and 4 of the Appendix, respectively. Means for the lesion groups by days interaction can be seen in Figure 2 of the text.

Comparisons of the run-speed group mean differences for each of the 4 test days tended to parallel those of the choice-speed data in that the difference between groups on Day 1 ($p < .01$) and Day 2 ($p < .05$) differed significantly from that on Day 3. In addition, the difference

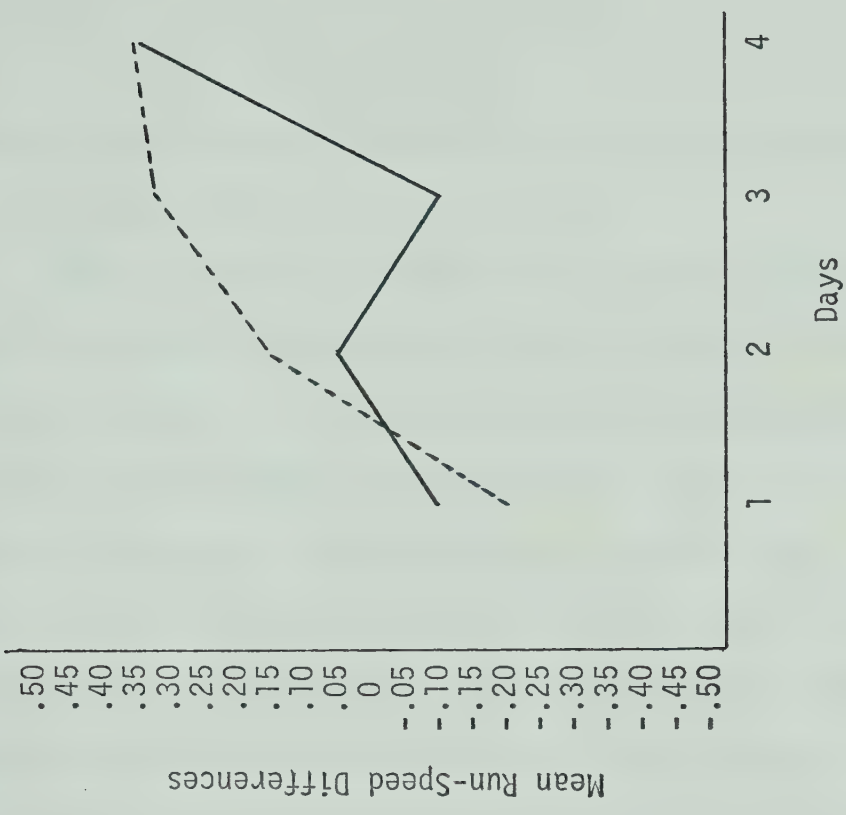
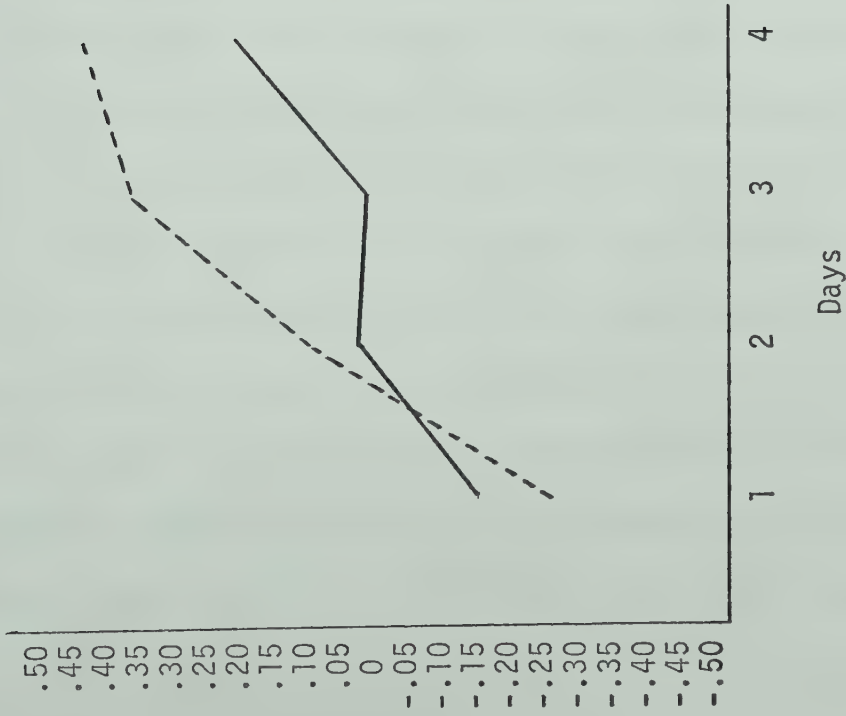


Figure 2

Mean differences between Pre- and Post-lesion Choice- and Run-Speed Scores per Day during Retention Testing. The solid line indicates MRF lesions on the Right. The interrupted line indicates MRF lesions on the Left.

between groups on Day 4 was seen to differ significantly from that on Day 3 ($p < .01$).

Since a correction procedure was used in this experiment, run-speed reflects not only the time taken to run from the choice point to the food cup, it incorporates the time taken to correct an error as well. Choice-speed, on the other hand, reflects, among other things, the degree of hesitation at the choice point. Though the interaction between lesion groups and days in error data was not significant, the direction of the differences tends to reflect the above interrelations in that the left lesion group made more errors on Day 1 and fewer errors on Days 2 and 3 than the right lesion group.

Discussion

In the analysis of difference scores arising from the retention test, a predicted error interaction was seen to be significant, i.e., the groups by side of reward interaction. Though this effect should be viewed with caution, it is consistent with the earlier finding that rats with unilateral MRF lesions tend to make more errors during the performance of a brightness discrimination task when reward is on the side opposite that of their lesion (Walley and Fedora, 1969; Walley and Weiden, 1969). Since this effect does not appear to interact with side of visual input, an explanation in terms of a perceptual deficit does not seem warranted. Alternatively, a deficit in the ability to perform appropriate motor movements to the side contralateral that of the MRF lesion seems a more likely hypothesis.

In considering both error and speed difference scores, however, it seems apparent that Ss were performing as well by the second day of post-lesion testing as they were before lesioning. As a consequence, it is suggested that whatever the effects of unilateral MRF lesions may be, they are not markedly detrimental to the performance of a simple pre-learned brightness discrimination problem.

Due to the lack of a non-lesioned control group, the interactions between experimental lesion groups and days in the choice- and run-speed data are difficult to interpret. The superior performance of the left lesion group over the right by the third day of testing may either suggest that MRF lesions contralateral to the side of visual input enhance performance during the retention of a simple brightness discrimination task, or that MRF lesions ipsilateral to the side of visual input suppress performance in such a situation. As will be noted, neither interpretation appears consistent with the notion of a contralateral visual field deficit.

Experiment 2

This experiment was designed to test for differences in performance between Ss with MRF lesions contralateral and ipsilateral to the side of visual input during a visually guided discrimination task similar to that used in Experiment 1. In the present experiment, however, the discrimination problem was made increasingly more difficult by manipulating the nature of the positive discriminandum.

Method

Subjects and Apparatus. The Ss and the apparatus were the same in this experiment as in Experiment 1, except that the mid-alley archways were removed leaving both correct and incorrect alley ways unobstructed. The only positive cue, therefore, was diffuse light from the large panel of flashed opal glass located at the end of the correct alley. In addition, Variacs were connected to the 25-Watt bulbs located behind the panels of flashed opal glass at the end of each alley. This modification allowed E to systematically manipulate the luminance emitted by the positive discriminandum.

Procedure. Two days after completing Experiment 1, Ss were run for 2 consecutive days in the modified apparatus. During this period, the luminance of the positive discriminandum remained the same as in Experiment 1. Data obtained on the dependent variables, i.e., errors, start-speed, choice-speed, and run-speed, were transformed as in Experiment 1 and subjected to the same 4-way analysis of variance design.

The luminance (as measured in foot-candles by a SEI Photometer) emitted by the positive discriminandum was then divided logarithmically into 6 steps and lowered one step per day for 6 consecutive days. These steps corresponded to 60.00, 47.75, 27.90, 18.00, 10.60, and 7.70 foot-candles, respectively.

Subjects were run under the latter conditions until they reached a drop-out criterion of 100% errors to one side on 2 consecutive days, or until they reached the sixth step. Errors transformed as in Experiment 1 as well as the number of days required to reach criterion were analyzed. Speed scores were not recorded.

Due to an unscheduled interruption, the last 6 days of this experiment began 18 days after completion of the first 2 days. During this interval Ss were housed in their home cages and allowed access to food and water on an ad lib schedule. Three days prior to commencing with the experiment, Ss were placed on a food deprivation schedule adjusted to maintain body weight at 85% normal, as in Experiment 1.

Results

In this experiment, data obtained during the first 2 days indicated that neither the right nor the left lesion group experienced any unusual difficulty in performing in the absence of the mid-alley archways. Speed scores during the same 2 days, however, did reveal a significant tendency for Ss to choose faster over trials ($F = 5.834$,

$\underline{df} = 4/56$, $\underline{p} < .01$) and run faster over days ($\underline{F} = 6.065$, $\underline{df} = 1/14$, $\underline{p} < .05$). Means for these effects can be seen in Tables 5 and 6 of the Appendix, respectively.

During the last 6 days of this experiment, no significant difference was found between groups in the number of days required to reach the drop-out criterion. Mean errors for right and left lesion groups, on the other hand, were found to be significantly different ($\underline{F} = 6.387$, $\underline{df} = 1/14$, $\underline{p} < .05$). The means for this effect were 2.033 and 2.383 for the right and left lesion groups, respectively.

Discussion

The absence of any significant differences in performance between side of lesion and side of reward indicates that any motor deficit that may have resulted from unilateral MRF lesions was not present to any marked degree in this experiment. On the other hand, when the luminance of the positive discriminandum was progressively lowered, Ss with MRF lesions contralateral to the side of visual input (i.e., the left lesion group) were seen to make more errors than those with ipsilateral lesions. As will be noted, this is the first clear indication of a perceptual deficit generated by MRF lesions.

The tendency for the contralateral group to make more errors than the ipsilateral group may be due directly to an inability of the contralateral preparations to discriminate small differences in luminance. On the other hand, a more subtle perceptual deficit may underlay this

finding. If it is reasoned that a discrimination task which becomes progressively more difficult demands a greater degree of attention and/or orienting activity than the mere retention of a relatively simple discrimination problem, then the results of this experiment are seen to be consistent with an hypothesis involving a decrement in attention and/or orienting activity to stimuli in the visual field contralateral that of the MRF lesion. In the following experiment, a discrimination task requiring S to pay attention to and/or orient to visual cues is examined while holding luminance constant.

Experiment 3

This experiment was designed to test for possible interactions between side of MRF lesion and side of visual input during the reversal of a simultaneous brightness discrimination task.

Method

The Ss and the procedure were the same in this experiment as in Experiment 1 except that: (1) the discrimination cues were reversed, i.e., light-off indicated the correct alley and light-on the incorrect alley; (2) there were only 8 trials per day instead of 10; and (3) Ss were run to a criterion of 15 correct trials within 2 consecutive days. Furthermore, the apparatus was modified from Experiment 1 by inserting doors of clear glass to replace the previously opaque mid-alley archway doors. This modification enabled light to be emitted through the lowered archway door of the incorrect alley, while at the same time preventing S from entering the end of that alley. The glass doors were cleaned and lowered in the incorrect alley before the start of each trial.

The present experiment was started 27 days after the completion of Experiment 2. During the interval between experiments, Ss were run for 21 days on a similar reversal discrimination problem except that the mid-alley archways were removed as in Experiment 2. This problem was abandoned in favor of the present problem, however, when no signs of reversal learning were observed during this period.

Results

In this experiment, no significant difference could be found between groups in the number of days required to reach criterion. There was, however, a significant difference between groups in mean number of errors committed during training ($F = 15.553$, $df = 1/14$, $p < .01$). As can be seen in Table 2, these means show that Ss tended to make more errors when reward was on the side contralateral that of their MRF lesion.

In the following analysis, only performance scores achieved over the last 5 days before reaching criterion were examined. This analysis was selected in order to maintain equal cell frequencies and sample at the same time a fairly homogeneous set of data. These scores were analyzed according to the same design and transformation procedures as described in Experiment 1. Range of days to criterion was 5-13.

Analysis of performance scores achieved over the last 5 days of reversal training showed lesion groups to differ significantly in start-speed ($F = 6.619$, $df = 1/14$, $p < .05$). The mean start-speed for right and left lesion groups was 685.725 and 335.161, respectively. Choice speed, moreover, showed a significant interaction between lesion groups and trials ($F = 3.508$, $df = 3/42$, $p < .05$). Means for this interaction can be seen in Figure 3. The interactions between lesion groups and trials was also seen in the run-speed data ($F = 3.482$, $df = 3/42$, $p < .05$) along with a significant lesion groups by days interaction ($F = 3.405$, $df = 4/56$, $p < .05$). Means for these interactions

Table 2

Mean Errors (per day) between Experimental Groups
and Side of Reward During Reversal Training.

Lesion Group	Side of Reward	
	Right	Left
Right	0.751	1.551
Left	2.160	0.596

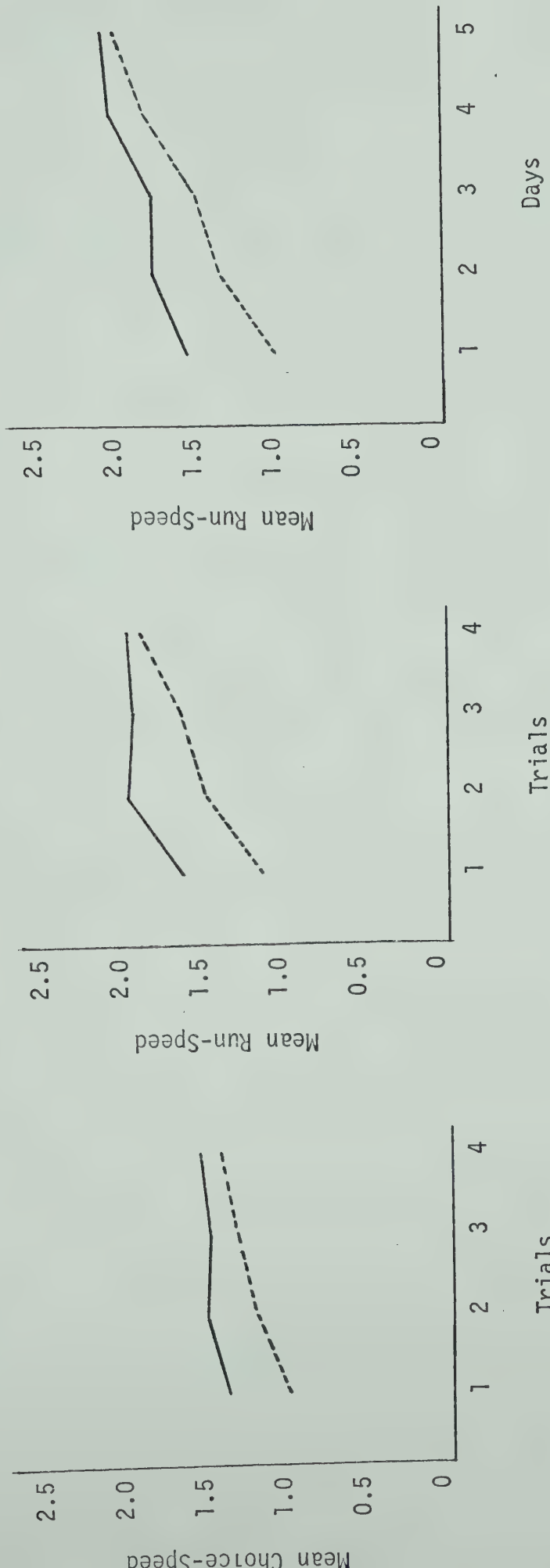


Figure 3

Mean Choice- and Run-Speed Scores by Trials or Days during the Last 5 Days of Reversal Discrimination Training. Trial 1 consists of the First Trial in which reward was on the Left plus the First Trial in which reward was on the Right, etc. The solid line indicates MRF lesions on the Right. The interrupted line indicates MRF lesions on the Left.

can also be seen in Figure 3. As can be seen, these data reveal a tendency for the left lesion group to: (1) start slower, (2) choose and run slower during the earlier trials of a session, and (3) run slower on the 3 days preceding the 2 criterion days than the right lesioned group. Taken together, these effects reveal a general tendency for the left lesion group to perform more poorly during reversal discrimination training than the right lesion group.

In addition to these findings, several effects of marginal interest were noted to be statistically significant during the last 5 days of training. There was, for instance, a decrease in the number of errors made over trials ($F = 4.045$, $df = 3/42$, $p < .05$) as well as days ($F = 42.756$, $df = 4/56$, $p < .01$). Means for these effects can be seen in Tables 7 and 8 of the Appendix, respectively. In addition, choice-speed was seen to increase significantly over trials ($F = 25.170$, $df = 3/42$, $p < .01$). Means for this effect can be seen in Table 7 of the Appendix. Run-speed showed a significant increase over trials ($F = 12.332$, $df = 3/42$, $p < .01$) and days ($F = 55.211$, $df = 4/56$, $p < .01$) plus a significant trials per days interaction ($F = 1.896$, $df = 12/168$, $p < .05$). Means for these effects can be seen in Tables 7, 8, and 9 of the Appendix, respectively.

In a final analysis, the area of the MRF lesion at its greatest extent was calculated for each S and correlated with mean individual performance scores achieved over the last 5 days of reversal training.

This analysis revealed a significant correlation between the size of lesion and start-speed for right lesioned Ss only ($r = 0.854$, $df = 7$, $p < .01$); the larger the lesion on the right the slower the start-speed. On the other hand, left lesioned Ss tended to start equally slow regardless of size of lesion. No significant correlations could be found between size of lesion and other performance measures in this or preceding experiments.

Discussion

The presence of a groups by side of reward interaction in mean errors committed during reversal training along with the absence of this effect when just the last 5 days of training were analyzed indicates that a positioning bias for the side ipsilateral that of the MRF lesion was present in the early stages of this experiment but absent as training progressed. The absence of a groups main effect in error scores in either analysis indicates that small unilateral MRF lesions do not markedly influence the rate of reversal of a brightness discrimination task when the visual field contralateral as opposed to ipsilateral to the side of the lesion is used. Moreover, the absence of a groups effect in the number of days required to reach criterion tends to support this conclusion.

On the other hand, the general decrement in speed scores by the experimental group with MRF lesions contralateral rather than ipsilateral to the side of visual input (i.e., the left lesion group) appears to indicate that a subtle perceptual deficit may result from

such lesions. The interaction between groups and trials in both choice- and run-speed scores indicates that this deficit has its greatest effect on performance during the early trials of a reversal discrimination training session. The interaction between groups and days in run-speed scores indicates that this deficit tends to influence performance to a greater degree during the earlier stages of training.

Though choice- and run-speed scores may be more sensitive measures of performance than error scores in this task (see discussion of these inter-relationships in Experiment 1), it is not easy to explain on the basis of either a perceptual or a motor hypothesis why start-speed is selectively influenced by the interaction between side of MRF lesion and side of visual input during reversal discrimination training. Possibly contralateral preparations start slower because of an inability to attend to visual cues associated with the start box door being lowered. The absence of this effect, however, in earlier experiments plus the presence of auditory and tactile cues argues against such an hypothesis. The high degree of correlation between size of MRF lesion and start-speed in the ipsilateral preparations tends to further complicate this finding. It should be noted that lesion size varied about the same for both lesion groups.

General Discussion

A review of the major findings in this study reveals that though small unilateral MRF lesions in the rat do not markedly interfere with the performance of a simple brightness discrimination problem learned prior to lesioning, Ss with lesions contralateral to the side of visual input show a greater increase in choice- and run-speed during the retention test than those with ipsilateral lesions. On the other hand, when the luminance of the positive discriminandum is progressively lowered the contralateral group tend to make more errors than the ipsilateral group. Moreover, during reversal discrimination training the contralateral group start slower, choose and run slower on the initial trials of a training session, and run slower during the earlier stages of training than the ipsilateral group. Taken together, these findings appear to suggest that unilateral MRF lesions affect the performance of visually guided tasks in a unique and subtle manner when such tasks are mediated by the visual field contralateral to the side of the lesion.

In addition, this study shows that MRF lesioned Ss tend to make more errors when reward is on the side opposite that of their lesion during the performance of a discrimination task learned prior to lesioning and during the early stages of reversal discrimination training than when reward is on the same side. This finding tends to support the notion that small unilateral MRF lesions in the rat

result in a preference for turning to the same side as that of the lesion. The severity of this effect, however, appears limited in that it was not observed during the progressive discrimination experiment or during the last 5 days of the reversal discrimination experiment.

An ipsiversive turning preference following unilateral lesions of the superior colliculus and underlying tegmentum has been reported in the cat by Sprague and his colleagues (Sprague et al., 1963; 1961; Sprague and Meikle, 1965) and in the rat by Cooper, Bland, Gillespie and Whitaker (1970). Schneider (1969) has observed a similar effect after undercutting the superior colliculus in the hamster. Several authors (Schneider, 1969; Sprague et al., 1963; Sprague and Meikle, 1965) have suggested that this behavior is the result of damage to fibers of the tectospinal tract; the final common pathway for motor movements of the head, neck, and trunk involved in visual orienting behavior (Sprague and Meikle, 1965). Since this tract passes through the MRF on its way to the ventral horn on the contralateral side of the spinal cord (Papez and Freeman, 1930; Rassmussen, 1935), it is suggested that the ipsiversive turning preference noted in the present study is the result of damage to these fibers. Moreover, the lack of severity of this effect may be a function of the limited damage to such fibers as a consequence of the very small MRF lesions used. This hypothesis is supported by the work of Skultety (1962) in which similar

MRF lesions in the cat resulted in ipsiversive turning, and by Sprague et al., (1963) in which lesions of the tectospinal tract after its decussation lower in the brainstem resulted in contraversive turning.

Discrepant findings have been reported, however, by Kesner et al., (1967) and Kesner and Vredenburg (1970). These experimenters have reported contraversive turning following unilateral MRF lesions in the rat. Though a satisfactory explanation regarding this discrepancy cannot be offered at this point, it should be noted that the MRF lesions in these latter experiments were quite large as opposed to those in the present study.

In attempting to explain the interactions between side of MRF lesion and side of visual input, at least three problems arise, First, the lack of a non-lesioned control group in the present study makes it difficult to determine which experimental group, the contralateral or the ipsilateral, is behaving abnormally. If, however, pre-lesion criterion performance can be taken as representing asymptotic performance for normal one-eyed rats, then it would appear that the contralateral group performs most unlike normals.

Secondly, the lack of a balanced design with regard to side of visual input tends to reduce the generality of the findings and calls into question the perceptual explanations offered so far. For example, Muntz and Sutherland (1964) have reported that monocularly discriminating rats tend to respond faster when stimuli are presented on the

same side as that of the visual field being used than when stimuli are presented on the opposite side. Though analysis of the pre-lesion data in the present study did not reveal this effect to be significant, pre-lesion performance means were in the direction specified by Muntz and Sutherland (1964). Combining the above tendency with a lesion produced preference for turning to the same side as that of the lesion, however, does not result in the type of interactions found in this study. That is, one would expect the ipsilateral group to perform best when reward is on the right and worst when reward is on the left as a consequence of combining the tendency to respond faster to stimuli on the right and the lesion produced preference for turning right. On the other hand, one would expect the contralateral group to be mixed in that they would tend to respond faster to stimuli on the right but prefer to turn to the left.

The third problem relates to the symmetry of the MRF lesions. As can be seen in Figure 1, the lesions appear to be relatively similar in size and general location. There is, however, a greater degree of variability in the location of the lesions on the right as opposed to those on the left. Though it is difficult to assess the functional consequences of this discrepancy, there are no apparent grounds for assuming that it would lead to the results noted in this study.

Given consideration of the problems of interpretation, it is nevertheless suggested that the interactions between side of MRF

lesion and side of visual input noted in this study can best be explained on the basis of a perceptual hypothesis involving visual attention and/or orienting activity. In general, it may be stated that the contralateral group performed more poorly than the ipsilateral group in both the progressive discrimination experiment and in the reversal discrimination experiment, but that in the retention experiment the contralateral group tended to perform better than the ipsilateral group. In examining the differences in task demands in the above experiments, it is argued that in the retention experiment successful performance did not depend upon orienting activity since, as Anokhin (1958) has found, orienting activity, though important in the initial stages of training, disappears once a conditioned motor response becomes established - unless conditions of the experiment change. On the other hand, in both the progressive discrimination experiment and the reversal discrimination experiment, successful performance involved the re-establishment of orienting activity to new or changing stimulus elements; the progressively decreasing luminance on the one hand, and the darkened alley on the other.

As a consequence of the absence of a performance decrement in the retention experiment, it is suggested that MRF lesions do not disrupt learned conditioned motor activities. In fact, the slight increase in performance by the contralateral group over the ipsilateral group as retention testing progressed may be the result of a reduction

in orienting activity to irrelevant stimuli in this group, i.e., to a reduction in competing responses. This hypothesis is supported by the findings that rats with bilateral MRF lesions perform a conditioned motor response of running down a runway learned prior to lesioning as well as normals, but that the same animals display less than normal orienting activity to novel stimuli presented during the performance of such a task (Kesner et al., 1970).

On the other hand, the greater number of errors committed by the contralateral as opposed to the ipsilateral preparations in the progressive discrimination experiment supports the hypothesis that MRF lesions interfere with the development of orienting activity to new or changing stimuli when the visual field contralateral to that of the lesion is being used. The greater reduction in run-speed by the contralateral as opposed to the ipsilateral group in the early stages of reversal discrimination learning lends further support to this hypothesis, since it is in the early stages of conditioning that orienting activities are seen to contribute to the development of the conditioned motor response (Anokhin, 1958). Moreover, the slower choice- and run-speed in the contralateral as opposed to the ipsilateral preparations during the initial trials of a reversal training session may be explained by the same hypothesis if it is reasoned that some orienting behavior is necessary on the initial trials of a training session.

The difference that was noted between groups in start-speed during reversal discrimination training, however, requires some further assumptions. Due to the fact that S could view the positive discriminandum prior to the start of a trial as a consequence of the clear plexiglass start box door, it is reasoned that such cues may have formed an important aspect of the stimulus situation in the start box and, in fact, actively supported the behavior of running out of the start box once the door was lowered. Secondly, since all Ss, before being trained on the present problem, received 21 days of training on a difficult reversal task without displaying any signs of learning, it is suggested that, prior to training on the present problem, the original positive discriminandum (i.e., light-on in one of the alleys) had become extinguished as an effective cue supporting starting behavior. As a consequence, the response of running out of the start box should have been impaired until the present positive discriminandum (i.e., the darkened alley) acquired cue value. Given that orienting activity facilitates the learning of a conditioned motor response to new cues, a disruption of visual orienting activity in the present experiment would result in retarded starting behavior. This being the case, the reduction in start-speed by the contralateral group over the ipsilateral group in the present reversal experiment may also be seen as the result of a reduction in orienting activity by this group to stimuli in the visual field contralateral that of MRF lesions.

The high correlation between the size of MRF lesions ipsilateral to the side of visual input and start-speed during the last 5 days of reversal discrimination training suggests that relatively large MRF lesions ipsilateral to the side of visual input also tend to impair orienting behavior. This could be due to interference with a pathway from the contralateral tectum to the ipsilateral MRF via the anterior tectal commissure (Pearce, 1958).

With regard to the nature of the orienting response deficit, two hypotheses are suggested. In the first case, the deficit in visually guided behavior arising from midbrain lesions may be the result of inability to perform appropriate orienting responses. Schneider (1969) has suggested this hypothesis and argues that it is the interruption of descending tectal fibers that cause this deficit. On the other hand, it may be argued that such lesions interfere with the role of the MRF as modifier of on-going neural activity (Scheibel and Scheibel, 1967) and thereby retard the development of the orienting response (Anokhin, 1958; Sokolov, 1960; 1958). In the first case it is the execution of the orienting response that is affected, whereas in the second it is the initial development of the central component of the orienting response that is affected. The neurological pathway mediating the latter effect may be the ascending reticular system described by Scheibel and Scheibel (1967). However, if this system receives visual input via descending tectal fibers, as hypothesized by Pearce (1958), deficits in visually guided behavior noted in

this study as well as those noted by Schneider (1969) and by Sprague and his colleagues (Sprague et al., 1963; 1961; Sprague and Meikle, 1965) may be due to either of the two mechanisms suggested since descending tectal fibers were interrupted in all cases.

In an attempt to replicate, in part, the findings of Sprague and Meikle (1965), Cooper et al. (1970) failed to find a perceptual deficit following either unilateral or bilateral lesions of the superior colliculus in the rat. Since damage to descending tectal fibers were involved in this experiment, this finding appears to weaken the foregoing arguments. It should be noted, however, that Cooper et al. (1970) only tested for retention of a simple visual discrimination problem learned prior to lesioning. As noted in the present study and by Kesner et al. (1970), midbrain damage does not appear to interfere with previously learned conditioned motor activity, but only with orienting activity that arises when changes in the experiment are made or when a new problem is introduced. As a consequence, no perceptual deficits would be expected in the study by Cooper, et al. (1970). Thompson (1969) reports similar negative results in visually guided behavior following superior collicular or MRF lesions, however, the same reasoning may apply here since he also tested only for retention of visual discrimination problems learned prior to lesioning.

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APPENDICES

Appendix

Table 1

Mean Error and Run-Speed Scores Per Trial During Pre-lesion Criterion Days (Trial 1 consists of the First Trial in which Reward was on the Right plus the First Trial in which Reward was on the Left, etc.).

Trials	Mean Error	Mean Run-Speed
1	0.756	1.996
2	0.731	2.214
3	0.707	2.264
4	0.723	2.239
5	0.707	2.201

Appendix

Table 2

Mean Run-Speed Scores Per Day
During Pre-lesion Criterion Days

Days	Mean Run-Speed
1	2.062
2	2.304

Appendix

Table 3

Differences in Pre- and Post-lesion Mean Error,
Choice-Speed, and Run-Speed Scores Per Day Dur-
ing Retention Testing.

Days	Mean Error	Mean	Mean
	Difference	Choice-Speed Difference	Run-Speed Difference
1	0.037	-0.210	-0.162
2	0.005	0.052	0.091
3	0.005	0.170	0.113
4	-0.005	0.314	0.335

Appendix

Table 4

Differences in Pre- and Post-lesion Mean Choice-Speed and Run-Speed Scores Per Trial During Retention Testing (Trial 1 consists of the First Trial in which Reward was on the Right plus the First Trial in which Reward was on the Left, etc.).

Trials	Mean Choice-Speed Differences	Mean Run-Speed Differences
1	-0.234	-0.121
2	0.117	0.193
3	0.194	0.187
4	0.167	0.150
5	0.164	0.063

Appendix

Table 5

Mean Choice-Speed Scores Per Trial During the First 2 Days of Experiment 2. (Trial 1 consists of the First Trial in which Reward was on the Right plus the First Trial in which Reward was on the left, etc.).

Trials	Mean Choice-Speed
1	1.781
2	2.091
3	2.127
4	2.137
5	2.224

Appendix

Table 6

Mean Run-Speed Scores Per Day During the First
2 Days of Experiment 2.

Days	Mean Run-Speed
1	2.334
2	2.505

Appendix

Table 7

Mean Error, Choice-Speed, and Run-Speed Scores Per Trial During the Last 5 Days of Reversal Training. (Trial 1 consists of the First Trial in which Reward was on the Right plus the First Trial in which Reward was on the Left, etc.).

Trials	Mean	Mean	Mean
	Errors	Choice-Speed	Run-Speed
1	0.843	1.098	1.367
2	0.840	1.297	1.638
3	0.820	1.341	1.728
4	0.788	1.399	1.815

Appendix

Table 8

Mean Error and Run-Speed Per Day During the Last 5
Days of Reversal Training.

Days	Mean Errors	Mean Run-Speed
1	0.950	1.214
2	0.865	1.537
3	0.836	1.565
4	0.739	1.866
5	0.723	2.003

Appendix

Table 9

Mean Run-Speed Per Day and Per Trial During the Last 5 Days of Reversal Training. (Trial 1 consists of the First Trial in which Reward was on the Right plus the First Trial in which Reward was on the Left, etc.).

Mean Run-Speed				
Days	Trial 1	Trial 2	Trial 3	Trial 4
1	1.215	1.180	1.100	1.360
2	1.174	1.577	1.686	1.710
3	1.206	1.574	1.654	1.885
4	1.484	1.882	2.074	2.025
5	1.757	2.036	2.126	2.092

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